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Semi-natural habitats support populations of stink bug pests in agricultural landscapes

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Abstract:	Semi-natural habitats are considered fundamental for biodiversity conservation and the provision of biological control services in agroecosystems. However, populations of crop pests that exploit and move across different habitat types during their life cycle might thrive in landscapes rich in semi-natural habitats. Understanding how crop pests use a range of resources across multiple habitats is fundamental to plan sustainable crop protection strategies in agricultural landscapes. Here we explored the effects of habitat type (i.e., annual crop, perennial crop, dry grassland and forest) and landscape composition (increasing cover of forest and dry grassland) on stink bug pests in Mediterranean agroecosystems. Stink bugs (Hemiptera: Pentatomoidea) are polyphagous and highly mobile organisms considered a serious threat for numerous agricultural crops worldwide. To better understand how stink bugs used different habitats, we sampled active adults and juveniles in spring and summer, and overwintering individuals in autumn and winter. Our results showed that semi-natural habitats supported more abundant stink bug populations, providing alternative feeding, reproduction, and overwintering sites. Specifically, we found more active adults and juveniles in dry grasslands, while forests hosted greater numbers of overwintering individuals. Moreover, forest cover in the landscape was positively related with active stink bug abundance in all sampled habitats, whereas landscapes rich in overall semi-natural habitats supported higher abundance of overwintering individuals in both forests and dry grasslands. These results have important implications for planning pest control strategies as crop fields situated in landscapes rich in semi-natural habitats might be more susceptible to pest infestation.
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Bari, 21th March 2022

Dear Editor,

We are pleased to submit the manuscript "**Semi-natural habitats support populations of stink bug pests in agricultural landscapes**" for consideration as a research article in *Agriculture, Ecosystems & Environment.*

Phytophagous stink bugs are considered key pests for several agricultural crops worldwide. Most species are polyphagous and highly mobile, which allow them to quickly move within agricultural landscapes. Even if some biological control agents are known to affect stink bug populations, their control is largely based on broad-spectrum insecticides with potential negative effects on the environment. Thus, identifying the main factors driving the population dynamics of these pests might inform more effective control strategies. Several studies investigated how stink bugs colonize crop fields from adjacent habitats, however little is known regarding stink bug habitat preference and response to landscape characteristics.

Here, we measured the abundance of both active and overwintering stink bug pests in four different habitat types in Mediterranean agroecosystems along a landscape gradient of semi-natural habitats. Our findings indicated that semi-natural habitats play an important role in supporting populations of stink bugs, with dry grasslands and forests providing potential alternative feeding, reproduction, and overwintering sites. Moreover, forest cover in the landscape was positively related with active stink bug abundance in all sampled habitats, whereas landscapes rich in overall semi-natural habitats supported higher abundance of overwintering individuals. These results might have important implications for pest control as crop fields situated in landscapes rich in semi-natural habitats might be more susceptible to pest colonization.

Considering the strong economic impact of stink bugs on agricultural production, our study provides significant implications for planning more eco-friendly stink bug control strategies, that consider pest dispersal across both crop and non-crop areas. Against this background, we hope that you will consider our study suitable for publication in *Agriculture, Ecosystems & Environment.*

We declare that none of the material has been published or is under consideration for publication elsewhere.

Best regards,

Ilaria Laterza (on behalf of the other co-authors)

Highlights

- We assessed the effect of habitat type and landscape composition on stink bug pests in agroecosystems
- Semi-natural habitats supported higher abundance of stink bugs than crop habitats.
- Dry grasslands and forests provided potential alternative feeding, reproduction, and overwintering sites.
- Landscapes rich in semi-natural habitats presented higher local abundance of both active and overwintering stink bugs.
- Crop fields situated in landscapes rich in semi-natural habitats might be more susceptible to pest infestation.

Semi-natural habitats support populations of stink bug pests in agricultural landscapes

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Abstract

Semi-natural habitats are considered fundamental for biodiversity conservation and the provision of biological control services in agroecosystems. However, populations of crop pests that exploit and move across different habitat types during their life cycle might thrive in landscapes rich in semi-natural habitats. Understanding how crop pests use a range of resources across multiple habitats is fundamental to plan sustainable crop protection strategies in agricultural landscapes. Here we explored the effects of habitat type (i.e., annual crop, perennial crop, dry grassland and forest) and landscape composition (increasing cover of forest and dry grassland) on stink bug pests in Mediterranean agroecosystems. Stink bugs (Hemiptera: Pentatomoidea) are polyphagous and highly mobile organisms considered a serious threat for numerous agricultural crops worldwide. To better understand how stink bugs used different habitats, we sampled active adults and juveniles in spring and summer, and overwintering individuals in autumn and winter. Our results showed that semi-natural habitats supported more abundant stink bug populations, providing alternative feeding, reproduction, and overwintering sites. Specifically, we found more active adults and juveniles in dry grasslands, while forests hosted greater numbers of overwintering individuals. Moreover, forest cover in the landscape was positively related with active stink bug abundance in all sampled habitats, whereas landscapes rich in overall semi-natural habitats supported higher abundance of overwintering individuals in both forests and dry grasslands. These results have important implications for planning pest control strategies as crop fields situated in landscapes rich in semi-natural habitats might be more susceptible to pest infestation.

Key words: Dry grassland, forest, Mediterranean agroecosystems, Pentatomoidea, Pest dynamics.

1. Introduction

Since the beginning of the Green Revolution, broad-spectrum pesticides have been widely used to try to control crop pests, leading to widespread environmental pollution and severe impacts on non-target organisms (Geiger et al. 2010). Moreover, agricultural expansion has resulted in landscape simplification, contributing to the decline of farmland biodiversity (Emmerson et al. 2016), further threatening the provision of important ecosystem services such as biological control of pests (Dainese et al. 2019). The implementation of integrated crop protection strategies that take advantage of natural regulation mechanisms have been largely advocated to reduce the negative impacts of agricultural production on the environment (Bianchi et al. 2006; Gagic et al. 2021). Identifying the main factors driving the dynamics of pest populations is crucial to support effective and more eco-friendly pest control (Mazzi and Dorn 2012).

Pest management strategies often focus on the local field scale. However, many pest species are mobile organisms that exploit and move across different habitat types during their life cycle (Kennedy and Storer 2000). Several studies have hence highlighted the need for considering larger scales and multiple habitats to better understand pest dynamics in agroecosystems (e.g., O'Rourke et al. 2011; Rusch et al. 2013). Semi-natural habitats embedded in agricultural matrices are known to influence pest populations both positively, providing alternative food resources, shelters, and overwintering sites (Cullum et al. 2020; Santoiemma et al. 2019; Tscharntke et al. 2016), and negatively, supporting populations of natural enemies such as predators and parasitoids (Holland et al. 2017; Mele et al. 2021). Although biocontrol is generally expected to be stronger in landscapes rich in semi-natural habitats (Bianchi et al. 2006), pest response to landscape composition in crop fields has been shown to be largely inconsistent (Delaune et al. 2021; Karp et al. 2018) and potentially driven by species-specific characteristics (Tamburini et al. 2020). Understanding how agricultural pests use a range of resources across multiple habitats and respond to landscape characteristics is fundamental to plan sustainable crop protection strategies beyond the field scale.

Phytophagous stink bugs (Heteroptera: Pentatomoidea) are responsible for important economic losses to agriculture on a global scale (Schaefer and Panizzi 2000). Stink bugs can cause major damage to important crops such as cotton, soybean, corn, rice, wheat, apple, kiwi, olive and cherry (Panizzi et al. 1997; Sosa- Gómez et al. 2020). Reductions in both yield quantity and quality are due to their feeding activity on fruits, seeds, leaves or stems (McPherson 2018; Panizzi 1997) and several species are also vectors of plant pathogens (Mitchell et al. 2018). Highly polyphagous and mobile species (e.g., the southern green stink bug, *Nezara viridula* L.) are considered particularly dangerous as they can move across the agricultural matrix feeding on both wild and crop hosts (Reeves et al. 2010; Schaefer and Panizzi 2000; Taki et al. 2014; Venungopal et al. 2014), often reinvading sites from which they were previously eliminated (e.g., Fauvel 1999). Previous studies explored how stink bugs colonize crop fields from adjacent habitats (Bundy and McPherson 2000; Tillman et al. 2009; Reeves et al. 2010; Venungopal et al. 2014, 2015) showing that semi-natural habitats, especially wooded ones, can support stink bug populations with alternative food and overwintering sites (e.g., under tree bark, in the leaf litter) (González et al. 2020; Lee et al. 2014a, 2015; Taki et al. 2014; Venungopal et al. 2014). Nevertheless, semi-natural habitats such as forests and riparian habitats have also been shown to support the biological control of some species of stink bug pests (Conti et al. 2020; González et al. 2017; Mele et al. 2021; Ogburn et al. 2016). It is hence important to better understand how stink bug pest populations use multiple habitats and their response to landscape characteristics.

The aim of this study was to explore the effects of habitat type and landscape composition on stink bug pests in Mediterranean agroecosystems. We measured stink bug abundance in four habitats characterizing the study region (i.e., annual crop, perennial crop, dry grassland and forest) along a landscape gradient of semi-natural habitats (increasing cover of forest and dry grassland). The four habitats provide different resources to stink bugs. Annual and permanent crops should both support pest populations by providing host plants during spring and summer. Forests are expected to mainly provide overwintering sites (Bakken et al. 2015). Dry grasslands should provide alternative host plants (especially when crops are harvested) and suitable reproductive sites (Panizzi 1997). To better understand how stink bugs use different habitats (i.e., as feeding, reproduction, or overwintering sites), we sampled active adults and juveniles in spring and summer, and overwintering individuals in autumn and winter. We hypothesized that i) semi-natural habitats would generally support stink bug pests, and that ii) forests would mainly be used as overwintering sites and dry grasslands for feeding and reproduction. We hence expected that iii) crop fields located in landscapes rich in semi-natural habitats would present more abundant communities of stink bug pests. We also tested whether species identity would influence stink bugs' response to habitat type and landscape composition.

2. Material and methods

2.1 *Study area, experimental set-up and landscape analyses*

The study was carried out in 2020 in the agricultural landscape of Bari and Barletta-Andria-Trani provinces in southeast Italy, within the boundaries of the Alta Murgia National Park. The park covers a total area of nearly 68,000 ha, and it is characterized by a Mediterranean semi-arid climate (mean annual precipitation = 700 mm, mean annual temperature = 15 °C) and it consists of extensively farmed areas interspersed with semi-natural habitats, such as dry grasslands, mainly used as extensive pastures, and forest patches (*Pinus halepensis* Mill. or *Quercus pubescens* Willd. forests). The arable land is cultivated with annual crops (mainly cereals and legumes), and perennial crops (mostly almond, olive and cherry).

We selected 12 non-overlapping circular landscapes with a 1 km radius along a gradient in the cover of semi-natural habitats (range =19 – 75 %, Fig 1). Landscapes were separated by at least 4.7 km, except for two that were located at shorter distance (3.78 km). To quantify the abundance of dry grasslands, forests and total semi-natural habitats within each landscape, we manually digitalized dry grassland and forest patches by visual inspection of high-resolution satellite images in Google Earth Pro (Google Inc.© 2017). We also measured landscape composition in a 2-km buffer in addition to the 1 km one, to test for potential scale dependence (correlations among landscape variables at different scales are presented in Table S1). Within each landscape we selected four sites representing the most abundant habitats in the region (i.e., annual crops, perennial crops, dry grasslands and forests) for a total of 48 sites. The annual crops were all wheat, the perennial crops were nine olive, one cherry and two stone fruit orchards, and the dry grasslands were all characterized by grasses and few shrubs (mostly *Scorzoneretalia villosae* Horvatić dry grasslands interspersed with *Pyrus spinosa* Forssk. trees). The forests comprised four oak and eight pine forests. The sites were distant a maximum of 370 m from the center of each landscape, except for two sites that were distant 580 m and 647 m, respectively.

2.2 *Insect sampling*

The survey was carried out from May to December 2020 across the 48 sites. We conducted two sampling campaigns to measure 1) the abundance of active stink bugs in spring and summer and 2) the abundance of overwintering adults in autumn and winter. Specifically, from May to September (five sampling rounds), specimens present on ground vegetation were collected using a sweep net on a total of six transects (100 m/transect) per site (three at the center and three at the edges). Moreover, since many stink bugs are pests of perennial crops, we selected six trees per site (three at the center and three at the edges) and we sampled the individuals present on the canopy, beating the branches and collecting insects on a white cloth placed underneath (beating technique). Trees were not present in annual crops, so the sampling on tree canopies was conducted only in perennial crops, dry grasslands and forests. However, because of the low number of specimens collected with the beating technique (32 specimens in total), only those collected by sweep netting were included in the analyses.

The second sampling campaign was conducted to identify those habitats used by stink bugs as overwintering sites. It took place from October to December (three sampling rounds) after the number of active individuals strongly decreased (see Results). We sampled both trees and leaf litter, as stink bugs typically overwinter as adults in sheltered environments such as litter or beneath the bark of trees and shrubs (Schwertner et al. 2021). At the center of each site, we removed and carefully examined the leaf litter from three randomly selected 1 x 1 m squares, and sampled three trees (the same plant species were surveyed during spring and summer) both with the beating technique and installing branch traps (i.e., a strip of cardboard mounted around one branch per tree that mimics tree bark; Schwertner et al. 2021). Branch traps were installed at c. 1.5 m of height, on branches similar in diameter (c. 15 cm) and checked monthly. This second sampling campaign was conducted only in perennial crop, dry grassland and forest habitats and not in annual crops, as these mostly presented bare soil and no trees or shrubs. Because of the low number of specimens found in the leaf litter (13 in total), only those collected on trees (i.e., via beating technique and branch traps) were included in the analyses.

After collection, insects were stored at -20°C until identification which was made following the main taxonomic keys of Heteroptera (Derjanschi and Péricart 2005; Lupoli and Dusoulier 2015; Ribes and Pagola-Carte 2013).

2.3 *Data analysis*

We used linear mixed-effects models to explore the effects of habitat type and landscape composition on the abundance of active and overwintering stink bug pests. We considered as landscape predictors the proportion of forest, dry grassland or total semi-natural habitats in the landscape at both 1 and 2 km scale. Six models were hence run per response variable (see below), each including a different landscape predictor (three habitat types at 2 different landscape scales). The model displaying the lowest AIC was considered as the best fitting model (Akaike 2011; Table S2).

For the analyses of active stink bug pests (first sampling campaign, from May to September), we averaged data at the site level for each sampling round, as preliminary analyses showed no effect of sampling location (center *vs*. edge; P = 0.928). We set up a total of three different models. With the first model (*model 1*) we explored the overall response of stink bugs to the tested factors. We hence included the total abundance of active stink bugs (both adults and juveniles) as response variable, and habitat type (categorical, four levels), landscape composition (continuous; % cover of forests, dry grasslands or total semi-natural habitats in the landscape), time (continuous; Julian days) and their interactions as predictors. With the second model (*model 2*), we explored whether adults and juveniles responded differently to habitat type and landscape composition. Stink bug abundance was hence averaged at the site level for adults and juveniles, separately. We included in the model the abundance of adult stink bugs for each development stage as response variable, and habitat type, landscape composition, development stage (categorical, two levels) and their interactions as predictors. We included also the quadratic and cubic terms of time in these first two models to better fit the temporal dynamics of stink bug populations. With the third model (*model 3*), we further tested whether species identity influenced stink bugs' response to the tested factors. Stink bug abundance was hence averaged at the site level for each species (i.e., time was not considered in this analysis to improve model residuals). We included in this model the abundance of adult stink bugs for each species as response variable, and habitat type, landscape composition, species identity (categorical) and their interactions as predictors. Juveniles were not considered for this analysis as they could not be all reliably identified at the species level. Species counting less than 30 individuals were not included in this analysis (Table S3). Standardizing stink bug abundance within species produced qualitatively similar results (not presented). For all three models, landscape and site ID were included as random factors.

For the analyses of overwintering stink bug pests (second sampling campaign, October to December) we averaged data at the site level (i.e., one record per site), as preliminary analyses showed no effect of sampling method (beating *vs*. branch traps) on the abundance of stink bug pests (P = 0.417). Time was not considered in this analysis to improve model residuals. The model (*model* 4) included the total abundance of overwintering stink bugs as response variable, and habitat type, landscape composition, and their interactions as predictors. Landscape ID was included as random factor. Stink bug abundance was log-transformed in all four models to abide by model assumptions.

Normality and homoscedasticity of the model residuals were validated graphically. All the analyses were performed in R using the 'lme4' package (Bates et al. 2017).

3. Results

During the first sampling campaign (from May to September) we collected a total of 1,645 adults belonging to 9 species of stink bug pests and 1,908 juveniles (Heteroptera: Pentatomoidea and Scutelleridae; Table S3). The most abundant species was *Eurygaster maura* L. (37.6%) followed by *Aelia acuminata* L. (15.9%), *Aelia germari* K. (12.0%) and *Dolycoris baccarum* L. (11.5%). Juveniles belonged mainly to the genus *Eurygaster* spp. (58.0%) and *Aelia* spp. (23.7%). During the second sampling campaign (from October to December) we collected a total of 112 overwintering adults belonging to 5 stink bug species. The most abundant overwintering species was *N. viridula* (58.0%) followed by *Piezodorus lituratus* F. (25.9%) and *D. baccarum* (8.0%) (Table S3).

Abundance of active stink bugs was influenced by both habitat type and landscape composition (Table 1). We found that the total abundance of active stink bugs (both adults and juveniles) was higher in dry grassland compared to the other habitats and that, after peaking in late spring, the total abundance declined (i.e., non-linear effect of time; Fig. 2A). However, forest habitat locally supported higher abundance of stink bugs at the end of the summer compared to annual and perennial crops (Habitat x Time interaction; *model 1*). When including development stage in the analyses (*model 2*), we found that juveniles were more abundant than adults at the beginning of the sampling period compared to late summer, but only in dry grasslands and forests (Habitat x Time x Development stage interaction; Fig. S1). We also found that habitat preference varied among species (Habitat x Species ID interaction, *model 3*; Fig. 3). Specifically, *E. maura* and *A. germari* were more abundant in dry grasslands, *E. austriaca* in annual crops, *E. ornata* and *D. baccarum* in both perennial crops and dry grasslands, whereas *A. acuminata* did not present clear differences. Including the proportion of forests at 2 km scale as landscape predictor always yielded the lowest AIC for all models on active stink bugs (Table S2). We found that the total abundance of active stink bugs increased with forest cover in the landscape in all the sampled habitats (*model 1*; Fig. 2B). However, the effect of landscape composition on stink bug abundance depended on the species identity (Forest x Species ID interaction, *model 3*): the positive effect of forest cover was observed for all the most abundant species except for *A. germari* which did not respond to landscape (Fig. S2). The effects of habitat type and landscape composition remained similar across models.

Abundance of overwintering adults was influenced by both habitat type and landscape composition (Table 1). We found that the abundance of overwintering stink bugs was generally higher in forest habitats, and that the effect of landscape composition depended on habitat type. The abundance of overwintering individuals increased with the proportion of semi-natural habitats (2 km scale), but only in forests and dry grasslands, whereas it showed the opposite trend in perennial crops (Habitat x Semi-natural habitats interaction, *model 4*; Fig. 4).

4. Discussion

Our study shows that semi-natural habitats play an important role in supporting populations of stink bug pests in Mediterranean agroecosystems. We found that stink bug pests were present in both crop and non-crop habitats, with dry grasslands and forests providing potential alternative feeding, reproduction, and overwintering sites. Agricultural landscapes rich in forests presented higher local abundance of stink bug pests in both crop and non-crop habitats, whereas landscapes rich in semi-natural habitats increased abundance of overwintering individuals in non-crop habitats. These results have important implications for the control of stink bug pests in agricultural landscapes, as crop colonization can be affected by the type and the abundance of semi-natural habitats in the surrounding landscape.

We found stink bug pests in both crop and non-crop habitats, confirming their ability to move across the agricultural matrix and to exploit a variety of habitats and hosts. Most of stink bug species are in fact polyphagous and highly mobile organisms (Lee et al. 2014b). Seasonal availability of resources probably influenced the temporal occurrence of stink bugs in different habitats (Bundy and

McPherson 2000; Tillman et al. 2009; Venugopal et al. 2014). Annual and perennial crops seemed to provide a suitable habitat for stink bug pests in spring and early summer, while abundance dropped in August and September. Similar seasonal trends were previously observed for true bugs in Mediterranean environments (e.g., Gessé et al. 2014), where severe late summer droughts can limit availability of host plants. Moreover, within our study area, cereals were harvested in June and herbaceous cover in orchards is often removed with machineries to avoid competition for water. Contrary to our expectations, we did not find any perennial crop specialist feeding on fruits in orchards after July, but only occasional pests of woody plants such as *D. baccarum* and *P. lituratus*, feeding on herbaceous plants (Mutlu et al. 2018). Besides, also the invasive alien pest Halyomorpha halys was not found in the surveyed sites despite the specie has been recorded in Apulia region in 2016 (Cianferoni et al. 2018). Dry grasslands presented the higher abundance of stink bug pests from May to September and resulted to be the favorite habitat for four out of the six most abundant species, i.e., *E. maura*, *A. germari, D. baccarum*, and *E. ornatum*. This is probably because dry grasslands provide more abundant, diverse, and temporarily stable communities of host plants (Malenovsky et al. 2011). Our findings confirm the importance of this habitat for stink bugs communities (Di Giulio et al. 2001; Gessé et al. 2014; Kőrösi et al. 2012) Interestingly, we found forests to present more abundant stink bug populations at the end of the summer compared to annual and perennial crops, suggesting that this habitat might provide aestivation opportunities and food resources not available in cultivated areas.

The semi-natural habitats in the study area represented also suitable reproductive sites for the populations of stink bug pests. We found more juveniles than adults at the beginning of the sampling period, but this difference was evident only in forests and dry grasslands and not in cultivated habitats (Fig. S1). This might indicate that stink bugs preferably used non-crop habitats for reproduction and development of juveniles (Panizzi 1997). Nevertheless, more studies are needed to better understand reproduction dynamics of stink bug communities in heterogeneous agroecosystems.

Our study also highlights the importance of wooded habitats as overwintering sites. We found higher abundance of overwintering adults in forests compared to dry grasslands and permanent crops. This is in accordance with previous studies that found this type of habitat to provide diverse shelter opportunities such as bark cavities, dense tree crowns and abundant soil litter (Jones et al. 1981; Lee et al. 2014a; Musolin 2012; Schaefer and Panizzi 2000). Contrary to our expectations, we only found overwintering stink bugs on trees rather than in the leaf litter. Moreover, we found no overwintering individuals of *E. maura* and *E. austriaca*, the first and fourth most abundant species in our study. Although expected to overwinter in large groups under dry leaves in forest habitats, *Eurygaster* species have been previously reported to migrate to elevated areas such as hills or mountains in late summer for both aestivation and hibernation (Brown 1965; Critchley 1998; Schuh and Weirauch 2020) potentially explaining the lack of overwintering *Eurygaster* individuals in our study. Nevertheless, our results also indicated that *Eurygaster* species positively responded to forest cover in the landscape (see below) indicating that this habitat plays an important role in the life cycle of this genus. More studies are needed to better understand the influence of specific thermal needs and of other landscape features (i.e., elevation; Cullum et al. 2020) on spatiotemporal dynamics of different pest species.

The importance of semi-natural habitats in supporting populations of stink bug pests emerged also when analyzing their response to landscape composition. We found that high cover of forests in the landscape was associated with high abundance of active individuals in all the surveyed habitats. Similar results were observed for stink bug pests in soybean in Argentina and for the brown-winged green bug, *Pautia stali*, in fruit orchards in Japan: severe orchard infestations were associated with high forest cover in the landscape (González et al. 2020; Taki et al. 2014). Also, at a smaller scale, many studies found both native and invasive stink bug species to move from woodlands to adjacent crops (Bakken et al. 2015; González et al. 2017; Bundy and McPherson 2000; Reeves et al. 2010; Tillman et al. 2016). As mentioned before, many Pentatomoidea species use forest habitats to search for alternative food and shelters (Schwertner et al. 2021), potentially playing an important role in stink bug life cycle and population build-up (Venungopal et al. 2014). We also found that abundant semi-natural habitats in the landscape (forests and dry grasslands) were associated with high numbers of overwintering individuals in forests and dry grasslands, but not in permanent crops. This is probably because the higher anthropic disturbance typical of cultivated crops, alters the optimal microclimatic condition required for overwintering (Cullum et al. 2020). Our analyses also showed that stink bugs best responded to landscape processes consistently at 2 km scale, confirming the available information in the literature regarding their dispersal ability (Olson et al. 2018; Taki et al. 2014). Finally, response to landscape composition was similar for the most abundant species except for *A. germari*, which showed no relationship with forest cover in the landscape. This pest of cereals might hence overwinter and find shelter in other type of habitats. Studies considering pest species identity might be required when planning specific control actions.

In conclusion, our study shows that semi-natural habitats play a key role in supporting the community of stink bug pests at multiple spatial scales in agroecosystems. This has important implications for pest control strategies: crop fields situated in landscapes rich in semi-natural habitats might be more exposed to pest invasion. Forests may potentially serve as source of overwintered adults colonizing fields and orchards in early spring, while dry grasslands as a season-long reservoir for crop infestations (Bakken et al. 2015; Cornara et al. 2021). Nevertheless, semi-natural habitats have been shown to support communities of natural enemies in agricultural landscapes (Dainese et al. 2019; Roland and Taylor 1997) and might contribute to the biological control of stink bug pests. For example, high forest cover in the landscape has been shown to promote the control of stink bugs in soybean without however reducing their abundance in the field (González et al. 2017, 2020). Moreover, Mele et al. (2021) recently found that both the abundance and the control by parasitoids of the invasive stink bug *Halyomorpha halys* in kiwifruit orchards, increased with the proximity to riparian vegetation. In this context, semi-natural habitats might be a greater source of pests than natural enemies (Bianchi et al. 2006, Tscharntke et al. 2016). Further studies are hence needed to better understand the role of semi-natural habitats in regulating stink bug communities in crops.

Improving knowledge regarding the factors driving stink bug population dynamics in agroecosystems could be useful to plan effective and sustainable pest management strategies aimed at reducing the use of pesticides (Grabarczyk et al. 2021; Taki et al. 2014). These strategies should consider pest dispersal across crop and non-crop areas and may require a landscape-based approach.

Declaration

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TABLES

Table 1. Results of the best fitting linear mixed-effects models (lowest AIC) testing the effects of habitat type (annual crops, perennial crops, dry grasslands, forests) and landscape composition (2 km scale) on the abundance of stink bug pests. Other fixed factors included were time (Days; model 1 and 2), development stage (Stage; model 2) and species identity (Species ID, model 3).

Variable	Chisq	P-value
1) Total stink bug abundance		
Habitat	**56.65**	**P < 0.001**
Forest (2 km scale)	**5.09**	**0.024**
Days	**16.82**	**P < 0.001**
Days^2	**17.82**	**P < 0.001**
Days^3	**17.79**	**P < 0.001**
Habitat : Forest	4.81	0.186
Habitat : Days	**13.24**	**0.004**
Forest : Days	0.13	0.714
Habitat : Forest : Days	3.51	0.320
2) Stink bug abundance (adults vs. juveniles)		
Habitat	**53.21**	**P < 0.001**
Forest (2 km scale)	3.77	0.052
Days	**27.59**	**P < 0.001**
Stage	**4.22**	**0.040**
Days^2	**28.30**	**P < 0.001**
Days^3	**27.42**	**P < 0.001**
Habitat : Forest	5.24	0.155
Habitat : Days	**15.54**	**0.001**
Forest : Days	1.12	0.290
Habitat : Stage	4.40	0.221
Forest : Stage	0.40	0.525
Days : Stage	**26.17**	**P < 0.001**
Habitat : Forest : Days	5.34	0.149
Habitat : Forest : Stage	0.10	0.992
Habitat : Days: Stage	**18.90**	**P < 0.001**
Forest : Julian days : Stage	0.56	0.455
3) Stink bug abundance (by species)		
Habitat	**30.83**	**P < 0.001**
Forest (2 km scale)	**4.97**	**0.026**
Species ID	**41.71**	**P < 0.001**
Habitat : Forest	2.11	0.550
Habitat : Species ID	**115.84**	**P < 0.001**
Forest : Species ID	**14.37**	**0.013**
Habitat : Forest : Species ID	6.36	0.973
4) Overwintering stink bug abundance		
Habitat	**10.24**	**0.006**
Semi-natural habitats (2 km scale)	0.26	0.613
Habitat : Semi-natural habitats	**7.42**	**0.024**

FIGURES

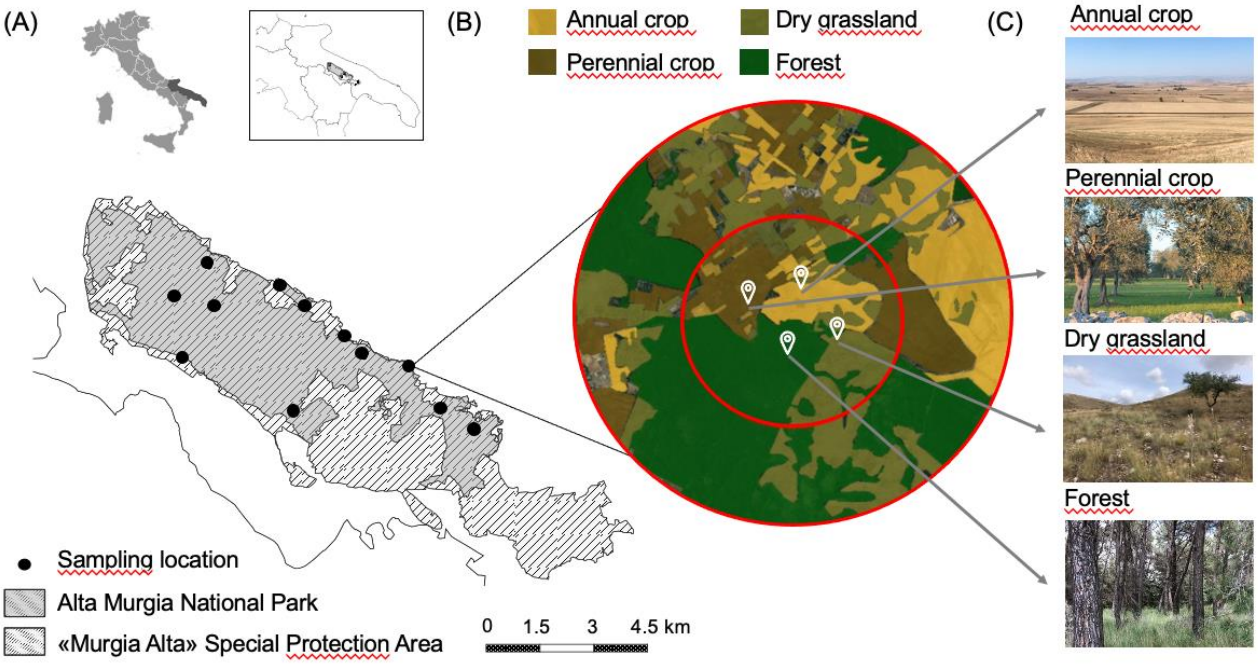

Figure 1. Map of the 12 sampling landscapes (A), example of landscape buffer at 1 and 2 km scale (B), and of the four investigated habitats within each landscape (C). (Color figure)

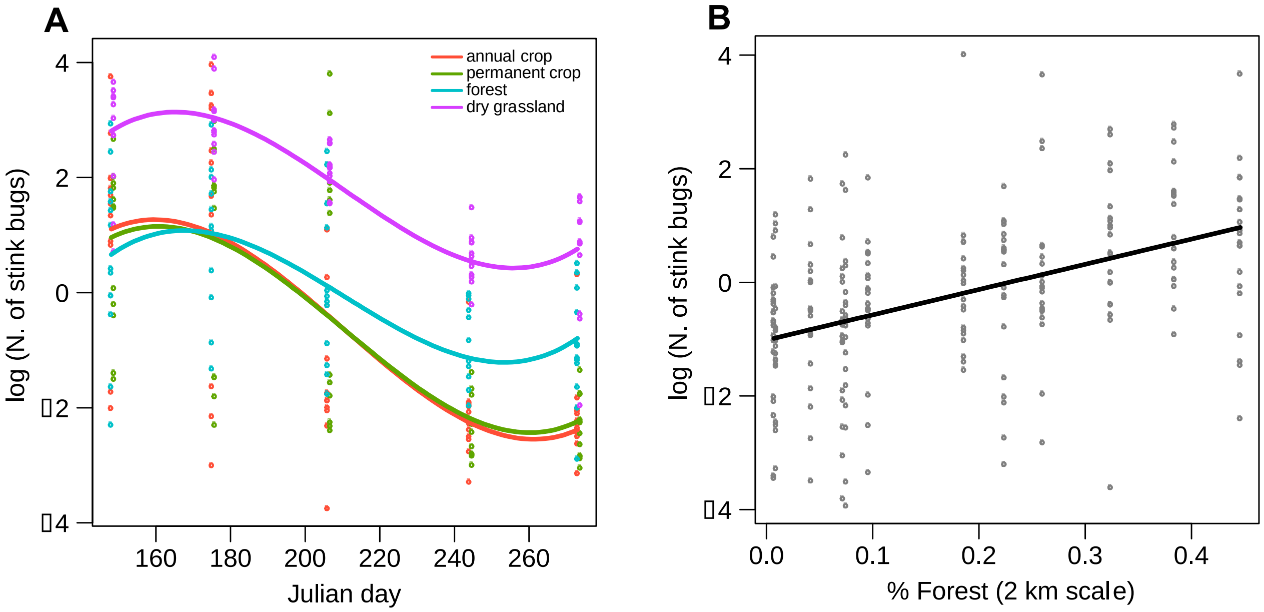

Figure 2. Effects of (A) time and habitat type and (B) landscape composition (% of forest cover at 2 km scale) on the overall abundance of stink bugs (i.e., both adults and juveniles) during the first sampling campaign (May-September) (*model 1*). Plots display prediction lines and partial residuals. (Color figure)

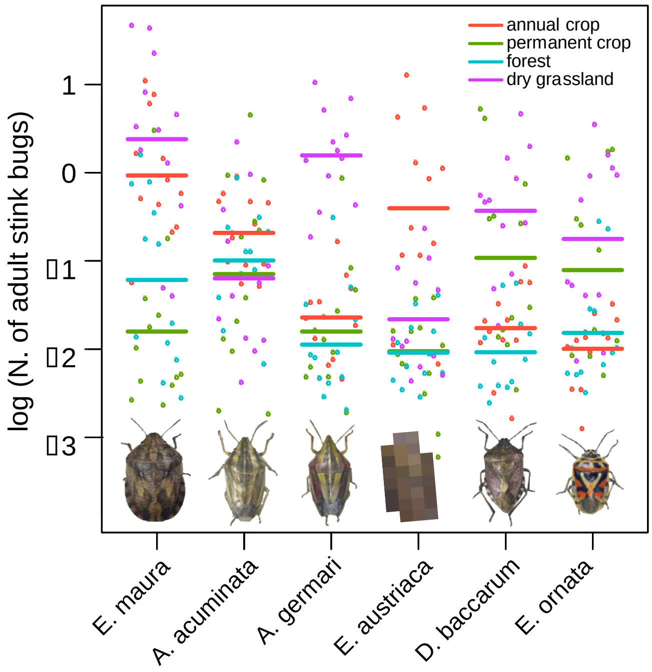

Figure 3. Habitat preference of the most abundant stink bug species collected during the first sampling campaign (May-September) (*model 3)*. Plots display prediction lines and partial residuals. (Color figure)

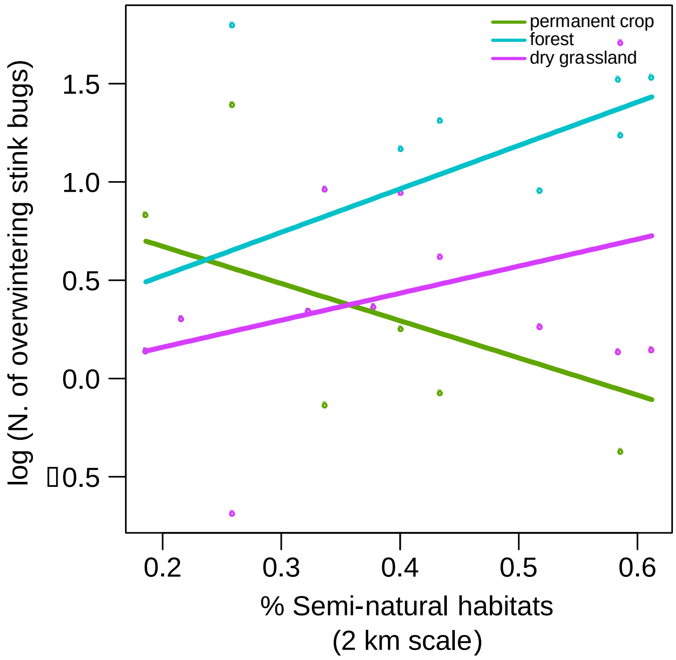

Figure 4. Effects of habitat type and landscape composition (% of semi-natural habitat cover at 2 km scale) on the abundance of overwintering stink bugs (second sampling campaign, October-December) (*model 4*). Plots display prediction lines and partial residuals. (Color figure)

Supporting Information

Semi-natural habitats support populations of stink bug pests in agricultural landscapes

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Table S1. Pearson correlations between landscape variables.

	Forest (1 km)	Forest (2 km)	Dry grassland (1 km)	Dry grassland (2 km)	Semi-natural (1 km)
Forest (2 km)	**0.87*****	-	-	-	-
Dry grassland (1 km)	-0.24	-0.39	-	-	-
Dry grassland (2 km)	-0.21	**-0.49.**	**0.90*****	-	-
Semi-natural (1 km)	**0.80***	**0.58***	0.39	0.36	-
Semi-natural (2 km)	**0.70***	**0.56.**	0.46	0.45	**0.94*****

. $P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Table S2. Results of model selection for selecting the landscape predictor and the scale to use for the different models. Models were run including the cover of forests, dry grasslands and semi-natural habitats in the landscape at two spatial scales (1, 2km) separately, and compared using the Akaike Information Criterion (AIC). The lowest AIC score is in bold.

Landscape predictor	Scale	AIC
1) Total stink bug abundance		
Forest	1 km	651.05
Forest	**2 km**	**647.24**
Dry grassland	1 km	659.10
Dry grassland	2 km	654.87
Semi-natural habitats	1 km	657.32
Semi-natural habitats	2 km	654.97
2) Stink bug abundance (adults vs. juveniles)		
Forest	1 km	1158.40
Forest	**2 km**	**1147.85**
Dry grassland	1 km	1169.52
Dry grassland	2 km	1165.84
Semi-natural habitats	1 km	1169.94
Semi-natural habitats	2 km	1167.69
3) Stink bug abundance (by species)		
Forest	1 km	801.97
Forest	**2 km**	**795.14**
Dry grassland	1 km	809.40
Dry grassland	2 km	809.10
Semi-natural habitats	1 km	804.87
Semi-natural habitats	2 km	797.08
4) Overwintering stink bug abundance		
Forest	1 km	86.96
Forest	2 km	87.56
Dry grassland	1 km	81.44
Dry grassland	2 km	83.25
Semi-natural habitats	1 km	83.18
Semi-natural habitats	**2 km**	**81.40**

Table S3. List of collected species during the two sampling period (active adults: May- September, overwintering adults (October- December) and details on host preference. Number of juveniles are not presented as they could not be all reliably identified at the species level.

Species	**Total number of active adults**	**Total number of overwintering adults**	**Host plant**
Eurygaster maura L.	618	0	Wheat and wild graminaceous species.
Aelia acuminata L.	262	6	Wild and cultivated graminaceous species.
Aelia germari Küster	198	0	Wild and cultivated graminaceous species.
Dolycoris baccarum L.	189	9	Wheat, barley, legumes (soybean, lentil and other), sunflower, hazelnut, strawberries.
Eurygaster austriaca austriaca Schrank	187	0	Wheat, oat.
Eurydema ornata L.	171	3	Brassicaceae, Asteraceae, Asteraceae, Fabaceae
Piezodorus lituratus Fabricius	28	29	Legumes (soybean, lentil), peach, almond, pome fruit, hazelnut, gorse, broom, *Genisteae* spp. woody.
Aelia rostrata rostrata Boheman	19	0	Wild and cultivated graminaceous species, grape, mulberry, tomato, pepper.
Nezara viridula L.	5	65	Highly pholyphagous.

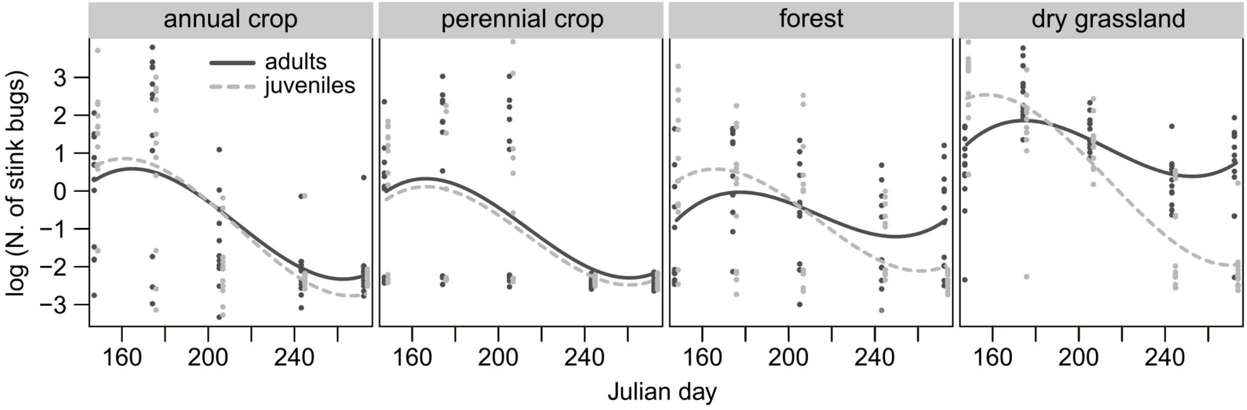

Figure S1. Effects of time and habitat type on the abundance of stink bugs for both adults and juveniles (i.e., effect of development stage) during the first sampling campaign (May-September) (*model 2*).

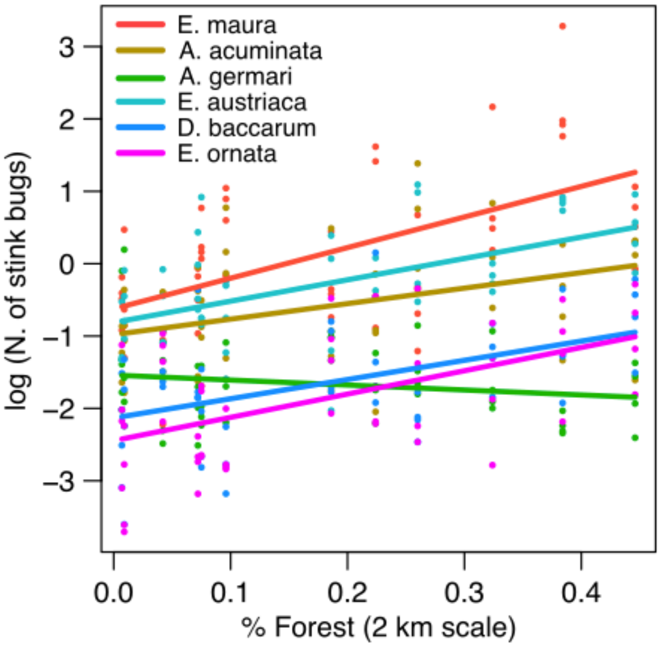

Figure S2. Effects of landscape composition (% of forest cover at 2 km scale) and species identity on the abundance stink bug adults during the first sampling campaign (May- September) (*model 3*).

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: